SYSTEMATIC POSITION OF THE AUSTRALIAN FOSSIL OSTEOGLOSSID FISH †*PHAREODUS* (=*PHAREOIDES*) *QUEENSLANDICUS* HILLS

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Li G.-q. 1994 12 01: Systematic position of the Australian fossil osteoglossid fish † *Phareodus (Phareoides) queenslandicus* Hills. *Memoirs of the Queensland Museum* **37**(1): 287-300. Brisbane. ISSN 0079-8835.

The Australian Tertiary teleost †*Phareoides* Taverne is a synonym of the fossil osteoglossid genus †*Phareodus*. Thus, †*Phareoides queenslandicus* is a junior synonym of †*Phareodus queenslandicus*. This Australian species of †*Phareodus* is phylogenetically most closely related to †*P. encaustus* from North America. The relationship is mainly supported by the frontal consisting of a narrow posterior portion and a greatly expanded anterior portion, the hyomandibular bearing a stick-like opercular process and a subtriangular anterior wing, the number of dentary teeth, the preopercle with an indistinct horizontal arm, and the pattern of the posterior infraorbitals. □ †*Phareoides*, †*Phareodus*, *synonym, Australia, North America, Lower Tertiary.*

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†*Phareodus queenslandicus* is a fossil osteoglossid named by Hills (1934) on the basis of materials from the Redbank Plains Formation of southern Queensland, Australia. It was considered to be similar either to the North American †*Phareodus acutus* [=†*Phareodus encaustus* (Cope) 1872, see Grande (1984) and this paper] in body shape and in the skull roof, or to the extant Australian *Scleropages leichardti* Günther, 1864 in the shape of the "post orbitals." Hills (1958) further believed that †*P. queenslandicus* might be the forebear of the Australian extant *Scleropages*. Roellig (1967) reached an opinion agreeing with Hills after his examining both fossil and extant osteoglossids. In contrast, Taverne (1973, 1974, 1978) asserted that †*P. queenslandicus* differs as much from the North American †*Phareodus* species as it does from †*Brychaetus* Woodward 1901; he thus coined another generic name, †*Phareoides* (see Taverne, 1973), for †*Phareodus queenslandicus*.

Recently, the Queensland Museum offered me an opportunity to reexamine specimens of †*Phareoides queenslandicus*. My examination yielded sufficient new information to allow a reassessment of the systematic position of this Australian fossil osteoglossid.

Specimens included in this study consist of fossils, dried skeletons of extant material, preserved, or cleared and stained extant specimens. All exclusively fossil taxa are marked with daggers (†) preceding their names throughout this paper.

MATERIALS

HIODONTIDAE: *Hiodon tergisus* Lesueur, specimens listed in Li & Wilson (in press). *Hiodon alosoides* (Rafinesque), specimens listed in Li & Wilson (1994). †*Hiodon consteniorum* Li & Wilson, specimens listed in Li & Wilson (1994). †*Eohiodon rosei* (Hussakof), UALVP12436 and specimens listed in Cavender (1966) and Wilson (1977). †*Eohiodon woodruffi* Wilson, specimens listed in Wilson (1978). †*Eohiodon falcatus* Grande, 14 specimens (FMNHPF9878-9880, 9882, 10424, 10633, 10634, 10639, 10955, 12516, 13063, 13064; ROM43220; and UALVP24203, SL ranging from 30 to 161mm). †*Yanbiania wangqingica* Li, specimens listed in Li (1987).

†LYCOPTERIDAE: †*Lycoptera davidi* (Sauvage), specimens including those listed in Liu et al. (1963), Ma (1987), and AMNHFF19400, 19403.

OSTEOGLOSSIDAE: *Osteoglossum bicirrosum* (Vandelli), one alizarin prepared specimen (UAMZ4642, SL = 177mm). *Osteoglossum ferreirai* Kanazawa, four alizarin prepared young specimens (UAMZ6753-6754, SL ranging from 48 to 61mm). †*Cretophareodus alberticus* Li, specimens listed in Li (in press). †*Phareodus testis* (Cope), 17 incomplete (AMNH743, 754, 805, 2467, 2471, and 8124; FMNHPF10241, 11939, 11941, 12412, 14061, 25439, and FMNHUF31; ROM28560, 29043 and 29076; UALVP12712) and 20 well-preserved (AMNH1336, 2799, 5821, 6301, 11547; FMNHPF10627, 10960, 10969, 11942, 11943, 12411, 12682, 13035, 13576, 25014, and

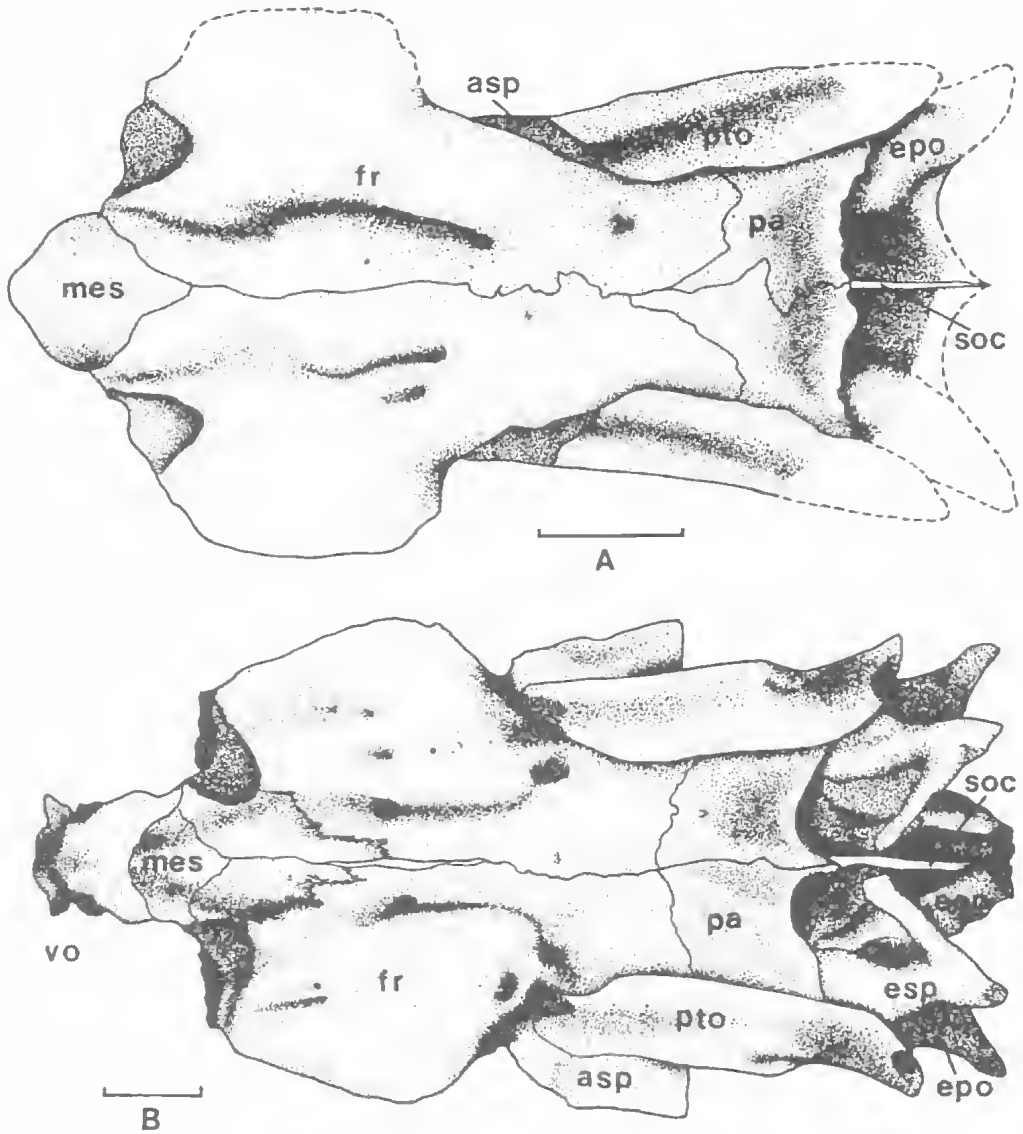

FIG. 1. Comparison of the skull roof between Australian and North American †*Phareodus* species. A, †*Phareodus queenslandicus*, QMF2917 (cast of UQF14960); B, †*Phareodus encaustus*, AMNH4587. Scale bars = 10mm. Note the "V-shaped" depression on the anterior margin area of each of the frontals, which receives the posterior end of the nasal in the two North American †*Phareodus* species as shown in Fig. 8 of this paper.

26407; UALVP447, 17657-17659. SL ranging from 39 to 304mm) specimens from the Green River Formation of Wyoming. †*Phareodus encaustus* (Cope), 16 incomplete (FMNHPF9891, 10255, 10257, 10963, 11938, 11952, 12515, 12683, 12685, 13103, 10961, 10962, 14064, and 14262; AMNH4587 and 8999) and 14 complete (FMNHPF10256, 10285, 10964-10967, 11944, 11954, 12408, 12409, 14040, 14062, 14063, 12681, SL ranging from 26 to 540mm) specimens from the Green River Formation of Wyoming. †*Phareodus queenslandicus* Hills, casts of specimens listed in Hills (1934); *Arapaima gigas* (Cuvier), one specimen (UAMZ2244, SL=285mm). †*Sinoglossus lushanensis* Su, specimens listed in Su (1986).

PANTODONTIDAE: *Pantodon buchholsi* Peters, one alizarin prepared specimen (UAMZ6751,

SL=72mm) and three specimens preserved in alcohol (UAMZ2273, SL ranging from 60 to 67mm).

NOTOPTERIDAE: *Chitala chitala* (Hamilton) (see Roberts, 1992), four alizarin prepared specimens (UAMZ6756, SL ranging from 72 to 82mm). *Xenomystus nigri* (Günther), two complete alizarin prepared specimens (UAMZ2272, SL=132; UAMZ6752, SL=125mm).

METHODS

The extant fishes are either fixed in formalin and preserved in alcohol or cleared and stained with alizarin (e.g. UAMZ3969). Measurements and counts were made mainly following Hubbs & Lagler (1964). Terms used for description follow Nelson (1968, 1969, 1973), Kershaw (1976), Wilson (1977), Patterson & Rosen (1977), Grande (1984), Li (1987), Arratia (1987), Arratia & Schultze (1991), Grande & Cavender (1991), and Wilson & Williams (1991).

ABBREVIATIONS

Institutional. AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; QM, Queeensland Museum, Australia; ROM, Royal Ontario Museum, Toronto, Canada; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada; UAMZ, Museum of Zoology, Department of Zoology, University of Alberta.

Anatomical. ang, angular; ao, antorbital; art, articular; asp, autosphenotic; boc, basioccipital; bpt. p, basipterygoid process on parasphenoid; br, branchiostegals; bs, basisphenoid; ch, anterior ceratohyal; clt, cleithrum; cm, coronomeckelian; den, dentary; d.hh, dorsal hypohyal; dsp, dermosphenotic; enp, endopterygoid; eoc, exoccipital; epo, epiotic; esp, extrascapular (supratemporal); fr, frontal; hm, hyomandibula; io1-5, 1st to 5th infraorbitals; mes, mesethmoid; mx, maxilla; na, nasal; op, opercle; os, orbitosphenoid; pa, parietal; pas, parasphenoid; pclt, postcleithrum; pmx, premaxilla; pop, preopercle; pt, posttemporal; pto, pterotic; pts, pterosphenoid; qu, quadrate; rart, retroarticular; sclt, supracleithrum; sm, symplectic; soc, supraoccipital; sop, subopercle; v.hh, ventral hypohyal; vo, vomer.

MEASURING AND MERISTICS

AFR, principal anal fin rays; AP, anal pterygiophores; CFR, principal caudal fin rays; DFR, principal dorsal fin rays; DP, dorsal pterygiophores; H, hypurals; SL, standard length; TV, total vertebrae.

SYSTEMATIC PALAEONTOLOGY

Subdivision TELEOSTEI Müller, 1846
Superorder OSTEOGLOSSOMORPHA Greenwood et al., 1966
Order OSTEOGLOSSIFORMES Berg, 1940
Family OSTEOGLOSSIDAE Bonaparte, 1850
Subfamily OSTEOGLOSSINAE

INCLUDED GENERA

†*Cretophareodus* Li (in press), †*Phareodus*, †*Brychaetus*, †*Singida*, *Osteoglossum*, and *Scleropages*.

EMENDED DIAGNOSIS

Osteoglossids differing from Heterotinae in the following features: palatine fused with ectopterygoid; tooth plates on basihyal and first to third basibranchials fused with each other to form an elongate basibranchial dentition; first pectoral fin ray particularly strong and long, with its distal end extending to beyond pelvic fin; horizontal arm of preopercle short, ending anteriorly far behind orbit; opercle subsemicircular in shape; preoperculo-mandibular canal in an open groove on horizontal arm of preopercle.

REMARKS

The genera included in this subfamily may also be characterized by having a hyomandibular with a subtriangular anterior wing, mandibulo-quadrate articulation lying far behind orbit, posterior end of maxilla extending back to level of quadrate condyle.

†*Brychaetus* Woodward, 1901 is osteologically similar to both †*Phareodus* Leidy, 1873 and †*Phareoides* Taverne, 1973. A comparison of the observable preserved cranial skeleton of †*Phareoides queenslandicus* with that of †*Brychaetus muelleri* (see Roellig, 1974) and †*Phareodus encaustus* suggests possible synonymy of both †*Phareoides* and †*Brychaetus* with †*Phareodus* (see discussion below).

†*Singida* Greenwood & Patterson, 1967 is included in the subfamily Osteoglossinae in this paper because it shares at least the following characters with the extant *Osteoglossum* and *Scleropages*: 1) The postero-ventral edge of the

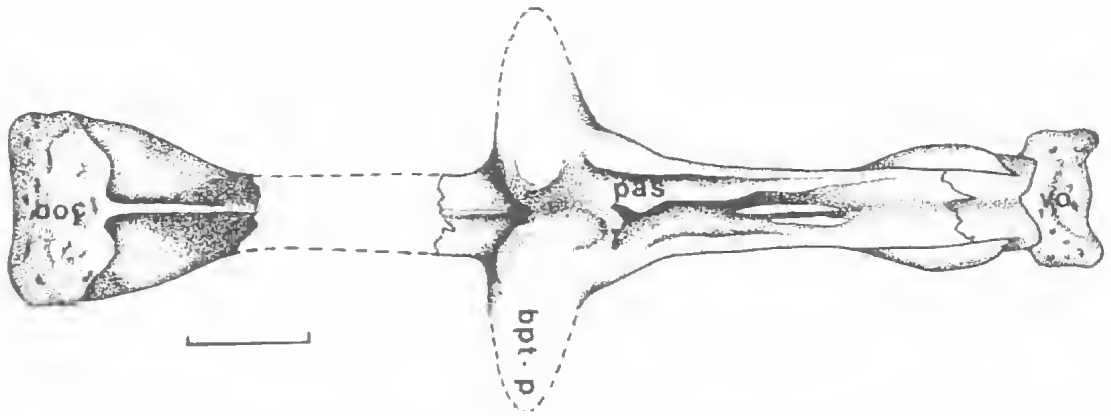

FIG. 2. Middle ventral part of the cranial base of †*Phareodus queenslandicus*, QMF2359a. Scale bar = 10mm.

opercle is distinctly concave. 2) The mandibulo-quadrate articulation lies far behind the orbit. 3) The mouth cleft is strongly upturned (Greenwood & Patterson, 1967). 4) Hypurals are reduced to five. These four characters indicate that †*Singida* is more closely related to *Osteoglossum* and *Scleropages* than it is to other genera in Osteoglossomorpha.

Genus †**Phareodus** Leidy, 1873

Osteoglossum Cope, 1872; 429; *Phareodus* Leidy, 1873: 99; Thorpe, 1938: 287; Hills, 1934: 160-164; Roellig, 1967: 137; Taverne, 1978: 7; Grande, 1984: 69;*Phareodon* Leidy; Cope, 1873: 637; *Dapedoglossus* Cope, 1877a: 807; Cope, 1877b: 570; Cope, 1883: 68-73; *Phareoides* Taverne, 1973: 497-499; Taverne, 1974: 724-734.

Type Species

†*Phareodus encaustus* (Cope, 1872) (= †*Phareodus acutus* Leidy, 1873).

Included Species

†*Phareodus encaustus* (Cope, 1872), †*Phareodus testis* Leidy, 1973, †*Phareodus* (=*Phareoides* Taverne, 1973) *queenslandicus* Hills, 1934.

Emended Diagnosis

Osteoglossinae differing from other genera in having the following features: frontal consisting of a narrow posterior portion and a laterally greatly expanded anterior portion, parasphenoid with teeth on posterior part, teeth on premaxilla ranging from 7 to 9 (never more than 9), depth to width of opercle ratio 2-2.5, first ural centrum bearing two complete neural spines, TV = 47-51, DFR = 16-21, DP = 18-24, AFR = 22-28, AP = 22-28, H = 5-6, CFR = 1-8-7-1.

†**Phareodus queenslandicus** Hills, 1934
(Figs 1A; 2; 3; 4A-B; 5A; 6A; 7A)

Phareodus queenslandicus Hills, 1934: 160-164, text-figs. 3-7; Hills, 1958: 100; Roellig, 1967: 43-49, 143-144, figs. 17-21; *Phareoides queenslandicus* Taverne, 1973: 497-499, fig. 1; Taverne, 1978: 25-32, figs. 15-19; Taverne, 1979: 123.

Diagnosis

†*Phareodus* differing from North American species mainly in having the combination of the following characters: suture between frontal and parietal antero-medially directed; dentary teeth about 27; ratio of depth to width of opercle about 2 to 2.5; origin of dorsal fin opposite origin of anal fin; TV = 46-49; DFR = 19; DP = 19; AFR = 26; AP = 26.

Holotype

QMF2357, a poorly-preserved specimen showing part of the cranial skelcton.

Referred Specimens

QMF2917 (cast of UQF14960), incompletely showing the skull roof (Fig. 1A); QMF2359, poorly-preserved part and conterpart, showing some of the cranial skeleton; QMF5754, showing part of the cranial skelcton; QMF2361, a poorly-preserved caudal region showing some scales and incomplete caudal fin rays.

LOCALITY AND OCCURRENCE

Redbank Plains, southeastern Queensland, Australia; Lower Tertiary, Redbank Plains Formation; Eocene to Oligocene.

REMARKS

Hills (1934), Roellig (1967), and Taverne (1978) have given a rather detailed description of this species, providing this study with valuable information. It is not necessary to redescribe all of the structures which were noted by those authors. This paper will emphasize those characters that I think are the most important for the phylogenetic analysis.

DESCRIPTION

Skull roof. QMF2917 (cast of UQF14960) shows a relatively well-preserved skull roof (Fig. 1A). The mesethmoid is rhomboid in dorsal view, inserting posteriorly between the anterior ends of the two frontals. The frontal is similar to that in †*Phareodus encaustus*, in which it is at least twice as broad anteriorly as posteriorly (Fig. 1). As in †*Phareodus encaustus*, a "V-shaped" depression that receives the posterior end of the nasal is present on the anterior margin of each of the frontals (Fig. 1). The suture between the frontals is relatively straight anteriorly but sinuous posteriorly. The parietal is irregular in shape with a length approximately 1/3 of that of the frontal. The suture between the two parietals is also sinuous.

Unlike the two North American species, the suture between frontal and parietal is anteromedially directed.

As in †*Phareodus encaustus*, the dorsally crested supraoccipital does not extend anteriorly to separate the posterior portion of the parietals.

Middle ventral part of cranial base. Judging from the remains on QMF2359a, the cranial base is structurally similar to that in the North American †*Phareodus* species. It consists of the vomer, the parasphenoid, and the basioccipital.

The vomer is somewhat shovel-shaped in ventral view with teeth on its anterior part.

As in the two North American †*Phareodus* species, the parasphenoid resembles a sword and bears strong basipterygoid processes (Fig. 2). However, teeth may be absent from the ventral side of this bone in the Australian species.

Opercular series. The bones comprising this series in †*Phareodus queenslandicus* are individually nearly identical to those in †*Phareodus encaustus* in both shape and proportions. The preopercle (Fig. 3) is slightly curved

FIG. 3. Preopercle of †*Phareodus queenslandicus*, QM F2359a. Scale bar = 10mm.

with an indistinct horizontal arm on which the preoperculo-mandibular canal opens in a groove (a synapomorphy of the subfamily Osteoglossinae). The opercle is subsemicircular in shape with a depth to width ratio about 2-2.5 (Fig. 4A,B).

Posterior infraorbitals. The two infraorbitals behind the orbit are almost identical to those in †*Phareodus encaustus* (Fig. 5A,B), consisting of one shallow (lower) and one deep (upper) element. The lower one is considered to be the third infraorbital, and the upper one the fused fourth and fifth. As in other osteoglossids, these two posterior infraorbitals cover the entire postorbital area between the posterior edge of the orbit and the preopercle.

Jaws. Both the upper and the lower jaws are virtually identical to those of the two North American †*Phareodus* species (Fig. 6). The maxilla is slightly dorsally curved with a relatively deep posterior portion and a tapering anterior end that overlaps the posterior part of the premaxilla. As in †*Phareodus encaustus*, a distinct dorsal swelling is also present on the anterior portion of the maxilla at the level behind the premaxilla. At least 26 conical teeth can be counted on the

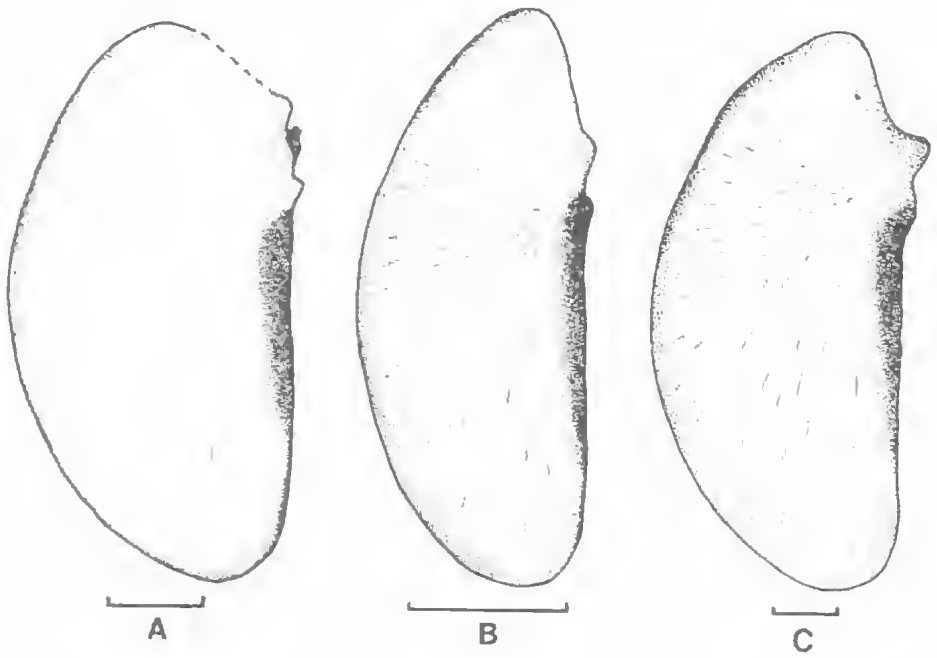

FIG. 4. Opercle. A,B, †*Phareodus queenslandicus*. A, QMF5754a; B, QMF2357. C, †*Phareodus encaustus*, FMNHPF12681. Scale bars: A, C = 10mm; B =20mm.

maxilla of QMF2357. A supramaxilla is absent. Taverne (1978: 26, fig. 15) labelled a supramaxilla in his illustration, but I am doubtful about that identification.

The dentary gradually deepens posteriorly and has a moderate coronoid process. This bone bears about 27 conical teeth that are larger than those on the maxilla and arranged in at least two rows.

A mesial (internal) view of the lower jaw (QMF2357) suggests a large triangular angular posterior to the dentary. Mesially adjoining this bone are an articular, which is irregular in shape and thicker posteriorly than anteriorly, and a small coronomeckelian. The retroarticular is identifiable on QMF2357, in which it is postero-ventral to the articular and angular. As in the North American †*Phareodus* species, the articular is not fused with the angular, and the articular facet for the quadrate is mainly on the articular (Fig. 6) (also see Nelson, 1973).

Hyoid arch. A complete hyomandibular is preserved in QMF2359a. This bone has a single head articulating with the cranium, a long postero-ventrally directed process articulating with the opercle, and a subtriangular anterior wing extending anteriorly as far as to the posterior rim of the orbit. A strong vertical ridge on the shaft of the hyomandibular extends from the head to the ventral tip where the bone articulates with the symplectic. This type of hyomandibular closely resembles that of †*Phareodus encaustus* (Fig. 7B).

DISCUSSION

SYNONYMY OF †*PHAREOIDES* WITH †*PHAREODUS*

When Taverne (1973: 497,498) established †*Phareoides*, he used 20 characters in its diagnosis: 1, Ostéoglossidé de grande taille (50cm), au corps court et trappu; 2, mâchoires ornées de grandes dents; 3, supraethmoïde hypertrophié; 4, naso-frontaux en contact médian; 5, expansions latérales externes de grande dimension dans la région naso-frontale; 6, pariétaux en contact médian et dénivelés en leur milieu; 7, ptérotiques étroits et très longs; 8, présence d'une fosse occipito-dorsale sur le pariétal, l'épiotique et le supraoccipital; 9, un supramaxillaire; 10, ptérygoïdes dentés; 11, hypertrophie des troisiéme et quatriéme infraorbitaires; 12, préoperculaire haut et large, à branche ventrale très réduite; 13, operculaire étroit mais très haut; 14, museau raccourci; 15, mandibule large et remontante; 16, premier rayon pectoral beaucoup plus fort que les suivants; 17, nageoires dorsale et anale très reculée sur le corps; 18, une cinquantaine de

vertèbres; 19, vertèbres abdominales à grandes hémapophyses situées transversalement; 20, écailles grandes, ornées d'une fine granulation et à radii en structure réticulée.

Among the above features of †*Phareoides*, none can be said to be an autapomorphy of this genus in the family Osteoglossidae. Character (1) is present not only in †*Phareodus*, but also in the recent *Osteoglossum*, *Scleropages*, and *Heterotis* if we count both the juveniles and the adults. Moreover, such variation in body size is of doubtful significance because we do not know how large the largest individuals of this Australian fossil species could be.

Character (2) is definitely a plesiomorphy. It is present in all of the extant and fossil genera of Osteoglossiformes (Ridewood, 1904, 1905; Taverne, 1977, 1978, 1979) except †*Singida* (Greenwood & Patterson, 1967). Large teeth on the lower and upper jaws can also be seen in most of the genera of Hiodontiformes (e.g., †*Yanbiania* Li, 1987; †*Eohiodon* Cavender, 1966; and *Hiodon* Lesueur, 1818) and many other teleosts (Gregory, 1933).

Character (3) needs to be clarified. Taverne's so-called "supraethmoïde" is synonymous with Hills' (1934) "mesethmoid" or Kershaw's (1976) "dermethmoid". I prefer using Hills' term to Taverne's "supraethmoïde" in this paper. This character is in fact shared at least by the two North American †*Phareodus* species. It should also be noted that Taverne's restoration of the naso-ethmoid region and his identification of the bones in this region of †*Phareodus acutus* [=†*Phareodus encaustus* (Cope, 1872) is incorrect. My recent examination of numerous specimens referred to †*Phareodus* from North America indicates that there is no such bone called "supraethmoïde" at the position labelled by Taverne (1973: 498, fig. 1) in either †*Phareodus encaustus* or †*P. testis*. His so-called "nasal" is also likely misidentified. At the place where Taverne labelled a "nasal", I can find only one bone that shows an appearance similar to his so-called "supraethmoïde" in †*Phareoides queenslandicus* (see Fig. 1). The true nasals, which could have been either missing from the specimens (FMNHPF14262) or disarticulated with the adjacent bones (FMNHPF12683), are separated from each other by the subrhomboid mesethmoid in the two North American †*Phareodus* species (see Fig. 8). I am also doubtful of Taverne's (1973, 1974, 1978) restoration for †*Brychaetus muelleri* (see Woodward, 1901). Judging from the illustrations provided by Woodward, that western European species may be also similar to the two North American †*Phareodus* species in the above aspects (pers. obs.).

Characters (4) and (5) are also in need of clarification. Hills (1934) made a mistake in identifying the frontal as the fused nasal plus frontal and labeling the anterior extension of the frontal as the "nasal" of †*Phareodus queenslandicus*. Taverne (1973, 1978) modified Hills' mistake,

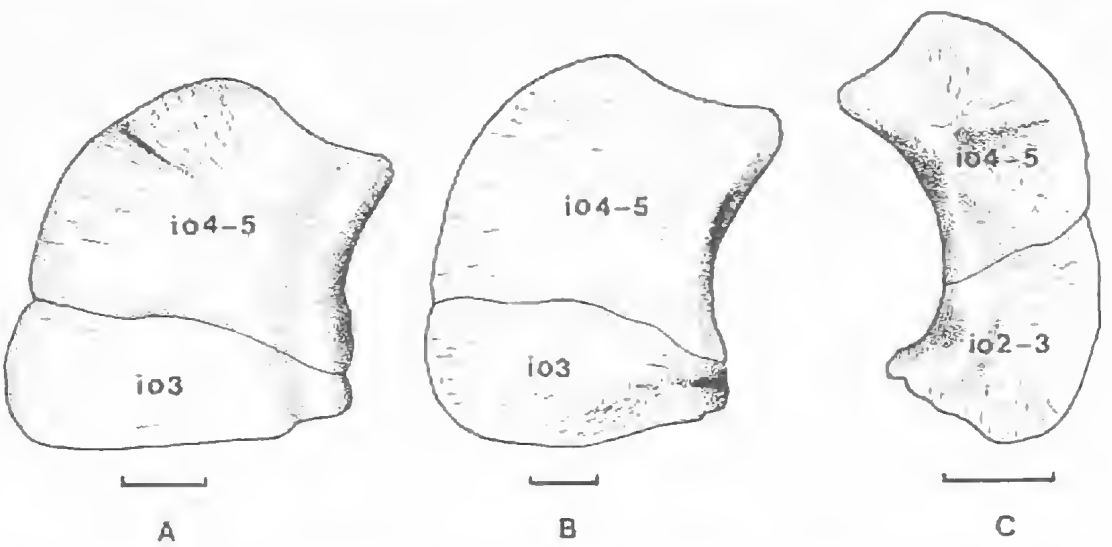

FIG. 5. Comparison of the posterior infraorbitals of †*Phareodus*. A, †*Phareodus queenslandicus*, QMF2357; B, †*Phareodus encaustus*, FMNHPF10256; C, †*Phareodus testis*, FMNHPF12682. Scale bars =10mm.

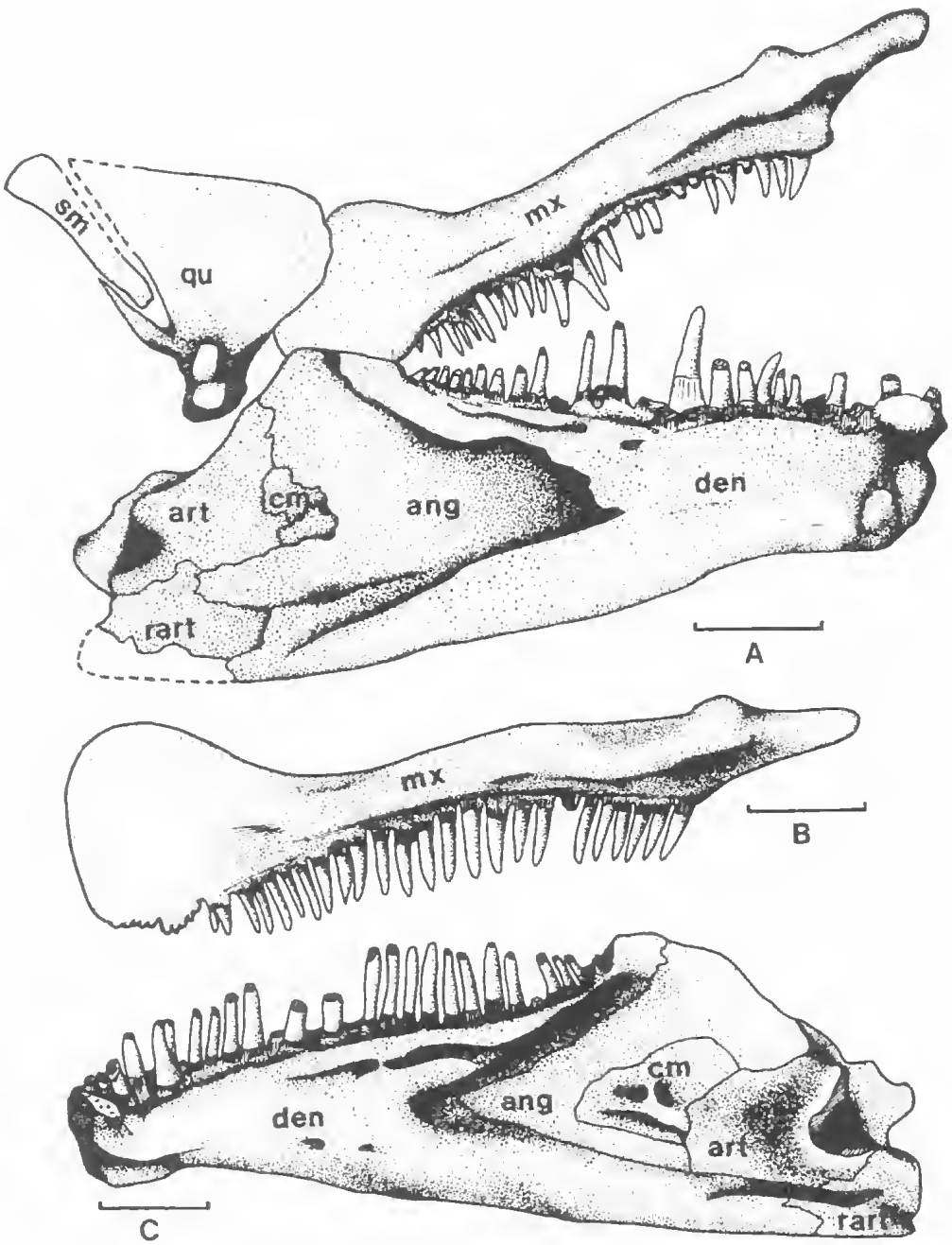

FIG. 6. Upper and lower jaws of †*Phareodus*. A, †*Phareodus queenslandicus*, QMF2357; B,C, †*Phareodus encaustus*. B, FMNHPF12683, C , AMNH2472. Scale bars = 10mm.

but he continued labeling the frontal and nasal as a fused "naso-frontaux" when he established †*Phareoides*. My study of the cast of UQF14960 suggests that the nasals are missing from the imen, leaving only a "V-shaped" depression on the anterior margin of each of the frontals, and that the two nasals are also separated from each other by the mesethmoid in this fish. The part

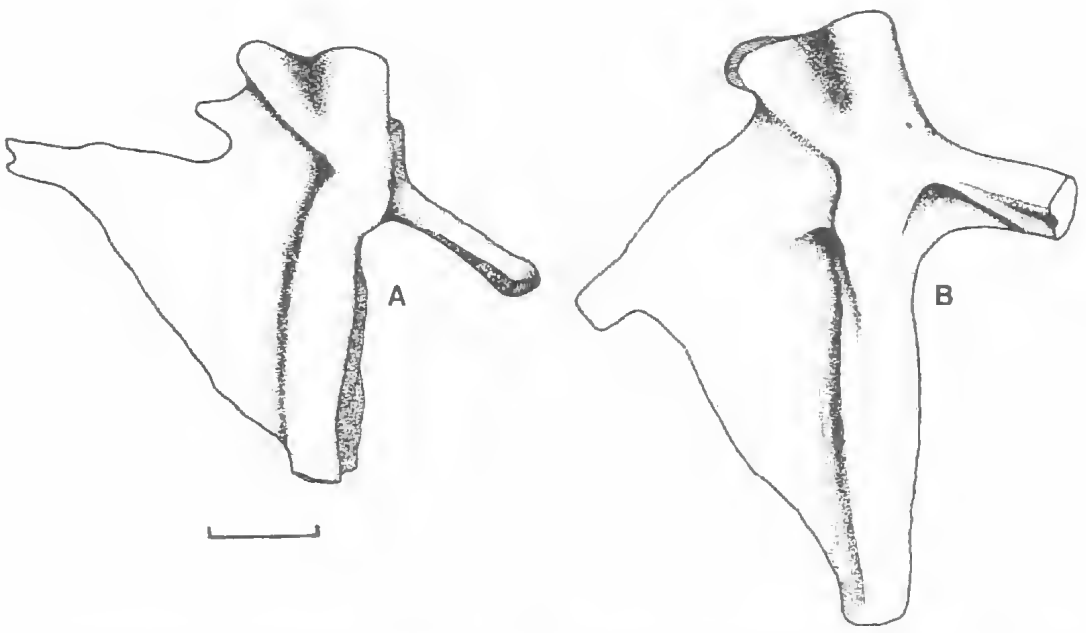

FIG. 7. Hyomandibular. A,†*Phareodus queenslandicus*, QMF2359a; B,†*Phareodus encaustus*, FMNHPF10285. Scale bar = 10mm.

labeled as the "nasal" by Taverne is, therefore, exactly the medio-anterior extension of the frontal (Fig. 1A). This situation is identical with that in the two North American †*Phareodus* species (see Fig. 1B). Therefore, Taverne's so-called "naso-frontaux" of †*Phareoides queenslandicus* consists only of the frontal. As illustrated by Taverne himself, the two frontals in †*Phareodus encaustus* and †*Brychaetus muelleri* are also medially sutured with each other and anterolaterally expanded. These two characters can thus only be considered to be synapomorphies shared by †*Phareodus*, †*Brychaetus*, and †*Phareoides*.

Character (6) is definitely not unique to †*Phareoides*. Parietals meeting with each other along the dorso-medial line can be seen at least in †*Phareodus*, †*Brychaetus*, the extant *Heterotis*, *Arapaima*, notopterids (Ridewood, 1904, 1905; Kershaw, 1976; Taverne, 1978), and all of the lycopterids and hiodontids (Ridewood, 1904; Greenwood, 1970; Taverne, 1977, 1978; Li, 1987; Li & Wilson, 1994). The only difference is that the suture between the two parietals is zig-zag-shaped in †*Phareoides* but nearly straight in the other genera mentioned above.

Character (7) refers to the pterotics. Although they are incompletely preserved on the specimen (Fig. 1A), the pterotics of †*Phareoides* are indistinguishable from those of the two North American †*Phareodus* species (Fig. 1B). In addition, elongate pterotics can also be seen in †*Brychaetus* (Woodward, 1901; Roellig, 1974; Taverne, 1978) and in the extant *Arapaima* (Ridewood, 1905; Kershaw, 1976). It is evident that this character is not unique to †*Phareoides*.

Character (8) defines a dorso-occipital fossa on the parietal, epiotic, and supraoccipital of †*Phareoides*. A similar depression is also developed in †*Brychaetus* (Taverne, 1978) and the two North American †*Phareodus* species (see Fig. 1B).

Character (9) suggests the presence of one supramaxilla in †*Phareoides*. My examination failed to confirm this bone in the specimens referred to †*Phareoides*. I believe Taverne's so-called "supramaxillaire" could be the posterior part of the endopterygoid.

Character (10) is related to the palato-pterygo-quadrate arch. In both the fossil and the extant osteoglossomorphs, toothed pterygoids (including ectopterygoid and endopterygoid) are commonly seen in most of the taxa of Osteoglossomorpha (Greenwood et al., 1966; Taverne, 1977, 1978). Therefore, †*Phareoides* can not be characterized by this plesiomorphy.

Character (11) describes the posterior infraorbitals of †*Phareoides*. In fact, †*Phareodus encaustus* shares this character with †*Phareoides*

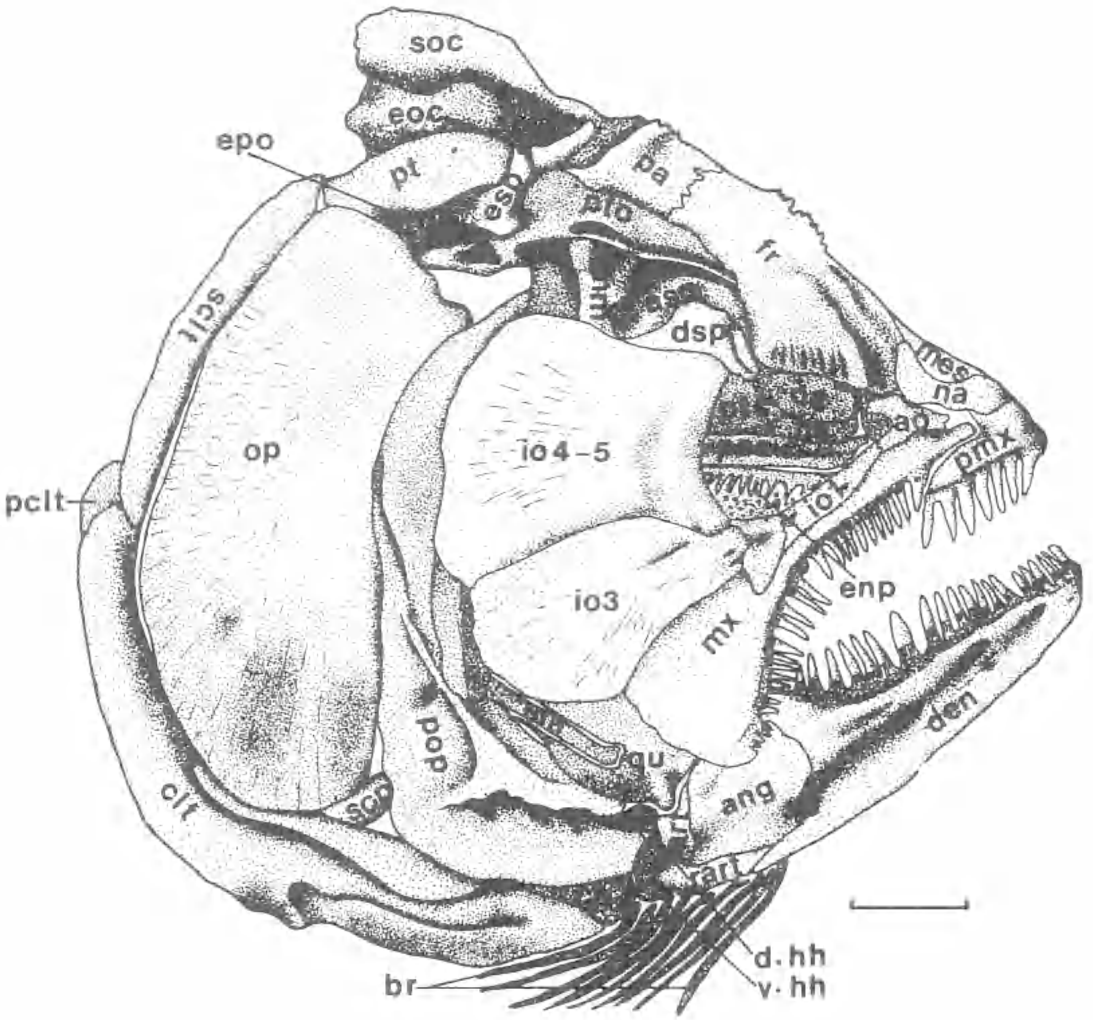

FIG. 8. †*Phareodus encaustus*. Line drawing of FMNHPF14040, showing the typical skull (cranial) characteristics of †*Phareodus*. Scale bar = 20mm.

(Fig. 5A-B). Similar posterior infraorbitals may also be seen in †*Brychaetus* (Woodward, 1901; Roellig, 1967, 1974; Taverne, 1978).

Characters (12) and (13) define the preopercle and opercle of †*Phareoides*. Using these two characters, I am not able to distinguish †*Phareoides* from all of the other genera grouped in the Osteoglossinae.

Character (14) is doubtful because the naso-oral region is poorly preserved on the specimens. Even if Taverne is correct, a reduced (short) naso-oral region can also be seen in the two North American †*Phareodus* species and the extant *Heterotis*.

Character (15) refers to the lower jaw. A detailed comparison suggests that the mandible in †*Phareoides* is almost identical with that in the two North American †*Phareodus* species in both structure and shape (Fig. 6).

Character (16) is one of the synapomorphies of the subfamily Osteoglossinae (Li, in press). Including †*Singida* (see Greenwood & Patterson, 1967), all of the genera in the subfamily possess a particularly strong first pectoral fin ray.

Character (17) is plesiomorphic for Osteoglossidae. Posteriorly located dorsal and anal fins are present not only in Osteoglossomorpha but also

TABLE 1. Comparison of †*Phareodus queenslandicus* with the two North American †*Phareodus* species, showing that all of the known meristic characters, as well as the ratio of opercular depth to opercular width, of †*Phareodus queenslandicus* are within the range of the two North American †*Phareodus* species.

	†*Phareodus encaustus*	†*Phareodus testis*	†*Phareodus queenslandicus*
Precaudal Vertebrae	22-25 (23)	22-25	~23
Caudal Vertebrae	25-27 (26)	24-28	~26
Total Vertebrae	47-51 (49)	47-52	~49
Branchiostegals	9-10 (10)	8-11	?
Pectoral Fin Rays	7-10	7-10	~6
Pelvic Fin Rays	4-6	4-6 (6)	~4
Principal Dorsal Fin Rays	17-22	16-20 (18)	~19
Dorsal Pterygiophores	18-24	18-21 (19)	~19
Principal Anal Fin Rays	22-25	24-28 (26)	~26
Anal Pterygiophores	22-26	24-28 (26)	~26
Caudal Fin Rays	17	17*	16
Hypural	5-6 (5)	5-6 (6)	?
Epural	1	1	?
Supraneural	22-26	22-26	?
Neural Spine on U1	2	2	?
Neural Spine on Pu2	1	1-2	?
Uroneural	0	0	?
Opercular Depth/Ocular Width	2-2.50	2-2.38	2-2.50

Numbers in brackets represent the most common situation within the range.
*16 on FMNHPF13576.

in some relatively primitive euteleosts (e.g. Esocoidei: Nelson, 1984, and pers. obs.).

Character (18), which gives the number of the vertebrae of †*Phareoides*, and (19), which defines the parapophyses, are shared also by the two North American †*Phareodus* species. My examination of the new North American fossils indicates that †*Phareodus encaustus* and †*P. testis* also have a vertebral column consisting of 47 to 51 centra (Table 1) and a pair of strong parapophyses on the abdominal vertebrae.

Character (20) describes the scales of †*Phareoides*. Reticulate scales with fine granular ornament are seen in all of the extant genera of Osteoglossidae (Lauder & Liem, 1983; Greenwood et al., 1966; Taverne, 1977, 1978) and in fossil †*Phareodus* (Cope, 1872, 1873; Leidy, 1873; Thorpe, 1938; Grande, 1984) and †*Sinoglossus* (Su, 1986).

To sum up, Taverne's diagnosis for †*Phareoides* does not characterize that genus. It is only a list of characters of †*Phareodus* mixed with characters of the family Osteoglossidae, the superorder Osteoglossomorpha, and other primitive teleosts. In fact, †*Phareoides* and †*Phareodus* are indistinguishable from each other in all of the 20 characters. This indicates that †*Phareoides* Taverne 1973 is a junior synonym of †*Phareodus* Leidy 1873.

PHYLOGENY OF †*PHAREODUS QUEENSLANDICUS*

Grande's (1984) study and my recent reexamination suggest that †*Phareodus* contains only two valid North American species: †*Phareodus encaustus* and †*P. testis*. The difference between these two North American species seems to be greater than the difference between †*Phareodus queenslandicus* and †*P. encaustus* (Table 1). Moreover, †*Phareodus queenslandicus* appears to be phylogenetically more closely related to †*P. encaustus* than it is to †*P. testis*. This hypothesis is supported by the following character states:

1. Anterior portion of frontal greatly expanded laterally. The frontal in †*Phareodus queenslandicus* is almost identical to that in †*Phareodus encaustus* in shape. In these two species the frontal has an anterior portion that is greatly expanded laterally, with a width at least twice as great as that of the posterior portion, or 1/2 of the length of this bone (Fig. 1). A frontal similar to that in †*Phareodus queenslandicus* and †*Phareodus encaustus* was supposed to be present in †*Brychaetus muelleri* by Roellig (1967, 1974) and Taverne (1978). My study suggests that there are too many discrepancies between Taverne's restorations and Woodward's (1901) original illustrations for that species. That makes me doubtful about Taverne's description of the frontal in †*Brychaetus muelleri*.

It is true that the frontals in some other osteoglossiforms (Greenwood & Patterson, 1967; Roellig, 1967; Kershaw, 1976; Taverne, 1977, 1978; Grande, 1984) are also anteriorly broader than posteriorly; however, none of them has an anterior portion twice as broad as the posterior portion (pers. obs.).

2. Hyomandibular with a stick-like opercular process and a subtriangular anterior wing.

Among the previously named fossil osteoglossids, such a hyomandibular has been seen so far only in †*Phareodus queenslandicus* (QMF2359 = RP/B-1 in Hills, 1934) and †*Phareodus encaustus* (Fig. 7). The stick-like opercular process in these two species is particularly long and forms an approximately equal angle with the lower vertical ridge of the hyomandibular. The subtriangular anterior wing extends anteriorly to the posterior edge of the orbit, ending in a distinct process that connects with the endopterygoid.

The hyomandibular in †*P. testis* bears a shorter opercular process but no distinct subtriangular anterior wing like that in the other two species.

3. Dentary bearing almost the same number of teeth. As shown in Figure 6, the dentary in both †*Phareodus queenslandicus* and †*P. encaustus* bears 27 large conical teeth. This coincidence can not be interpreted as a simple similarity between these two species. Most of the specimens referred to †*Phareodus encaustus* have 25 to 27 dentary teeth. This is also the estimate of the number of dentary teeth in †*Phareodus queenslandicus*. The teeth on the dentary of †*P. testis* are usually three to four fewer than those of the above two species. It seems to me that the number of dentary teeth may be phylogenetically informative although this significance should be further investigated.

4. Preopercle with an indistinct horizontal arm. In †*Phareodus queenslandicus*, the preopercle is moderately curved, with the upper part approximately as broad as the lower part (Fig. 3). No distinct horizontal arm can be seen in this species. This type of preopercle is basically the same as that in †*Phareodus encaustus* (Fig. 8). Although the preopercles in †*P. testis* (e.g. UALVP17658) and the extant *Osteoglossum* (e.g. UAMZ4642) are also shallowly curved in shape, they possess a distinct horizontal arm and a dorsally tapered vertical arm. Thus a moderately curved preopercle without a distinct horizontal arm may be another important character state linking †*Phareodus queenslandicus* with †*P. encaustus*.

5. Posterior infraorbitals (io3 and io4+5) in the same pattern. QMF2357 (Fig. 5A) and QMF5754 show two posterior infraorbitals of †*Phareodus queenslandicus*. The narrower lower one was considered to be the third infraorbital, and the broader upper one the fourth by Taverne (1978: 26, fig. 15). Among the other known osteoglossomorphs (Nelson, 1969), similar posterior infraorbitals are present only in †*P. encaustus* and possibly in †*Brychaetus* (pers. obs.). As shown (Figs 5, 8) †*Phareodus queenslandicus* and †*P. encaustus* are indistinguishable from each other in the pattern of the posterior infraorbitals.

CONCLUSIONS

1. Taverne's diagnosis for †*Phareoides* is only a list of characters of †*Phareodus* mixed with characters of the family Osteoglossidae and the superorder Osteoglossomorpha. In fact, †*Phareoides* and †*Phareodus* are indistinguishable from each other in all of the 20 characters listed in the diagnosis, indicating that †*Phareoides* is a junior synonym of †*Phareodus*.

2. The Australian †*Phareodus queenslandicus* is phylogenetically most closely related to †*P. encaustus* from North America. This relationship is mainly supported by the frontal consisting of a narrow posterior portion and a greatly expanded anterior portion, the hyomandibular bearing a stick-like opercular process and a subtriangular anterior wing, the number of the dentary teeth, the preopercle with an indistinct horizontal arm, and the pattern of the posterior infraorbitals.

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